NeoBiota 89: 161–186 (2023)
doi: 10.3897/neobiota.89.110203
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

The devil is in the details: exploring how functionally distinct round goby is among native fish in the Baltic Sea

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Academic editor: Belinda Gallardo | Received 28 July 2023 | Accepted 7 November 2023 | Published 22 November 2023

Citation: Vivó-Pons A, Wallin-Kihlberg I, Olsson J, Ljungberg P, Behrens J, Lindegren M (2023) The devil is in the details: exploring how functionally distinct round goby is among native fish in the Baltic Sea. NeoBiota 89: 161–186. https://doi.org/10.3897/neobiota.89.110203

Abstract

Understanding the characteristics and conditions that make non-indigenous species (NIS) successful at establishing in recipient communities is a key in determining their potential impacts on native species, as well as to improve management actions such as prevention of future invasions. The round goby (*Neogobius melanostomus*) is one of the most widespread non-indigenous fish species in the Northern Hemisphere, including the coastal zones of the Baltic Sea. The impacts of round goby in the Baltic Sea are pronounced and multifaceted, yet our knowledge regarding the underlying assembly processes determining its establishment is limited. To overcome this knowledge gap, we applied a trait-based approach to assess the degree of niche overlap and functional (trait) similarity between round goby and native fish species in coastal areas from the Baltic Sea, based on the functional distinctiveness metric. Our results show that round goby is generally quite similar (or not dissimilar) to the native fish of the regional species pool, at least in terms of its overall trait composition. Conversely, round goby demonstrates pronounced differences compared to the native community in its display of parental care and territorial behaviour. Such differences in individual traits could play an important role in round goby's invasion success in the Baltic Sea, including its interactions with native species (e.g. competition). Our results and their potential implications may be highly relevant for conservation and management if integrated within existing risk assessment tools for biological invasions in order to prioritise and enhance the effectiveness of preventative actions towards the expansion of round goby.

Keywords
Baltic Sea, biological invasions, coastal fish, functional distinctiveness, NIS, round goby, species traits, trait-based approach

Introduction

The introduction and spread of non-indigenous species (NIS) constitute a major threat to global biodiversity, ecosystems and their associated services (Bax et al. 2003; Millennium Ecosystem Assessment (Program) 2005; IPBES 2023). In marine ecosystems, the spread of NIS has increased during the last decades, largely due to increased global marine transport (Vitousek et al. 1996; Rilov and Crooks 2009). On a global scale, the impacts of such introductions are negative and may interact in a synergistic or additive way with other anthropogenic impacts (Anton et al. 2019; Geraldi et al. 2020). Yet, at local spatial scales, the effects of NIS can be highly diverse and context-dependent and even include neutral or positive effects (Katsanevakis et al. 2014; Viana et al. 2019; Vivó-Pons et al. 2020).

Before having an impact on native communities, NIS need to be successfully established in the recipient area with self-sustaining populations (Blackburn et al. 2011). The establishment depends on several community assembly processes (Gallien et al. 2015; Kraft et al. 2015; Montanyès et al. 2023) related to both abiotic and biotic factors. In communities heavily influenced by abiotic factors, species are expected to be functionally alike, with a common set of traits to be able to cope with the environmental conditions (Zobel 1997). Conversely, in communities mainly shaped by biotic factors, such as competition (i.e. limiting similarity), species tend to be functionally dissimilar or occupy more specialised niches (Gallien et al. 2014). Despite the conceptual understanding of NIS and the role of community assembly rules affecting their establishment, our empirical insight regarding the degree of niche overlap (i.e. functional similarity/dissimilarity) of NIS and native species is limited (Gallien and Carboni 2017), especially in marine ecosystems. For instance, it is debated whether NIS generally display similar or dissimilar traits compared to native species of recipient communities (Gallien and Carboni 2017) and to what degree the similarity or dissimilarity of NIS may affect their invasion success. Previous studies suggest that NIS both can establish by being functionally similar to natives (Cleland 2011; El-Barougy et al. 2020) or by being dissimilar to natives (Ricotta et al. 2010; Escoriza and Ruhí 2016; Mathakutha et al. 2019; Steger et al. 2022; Xu et al. 2022). Thus, disentangling the different assembly processes shaping communities and the niche overlap between NIS and native species' niches is fundamental to better understand biological invasions and their associated impacts on native communities and ecosystems (Ricciardi et al. 2013).

The Baltic Sea is one of the largest brackish water bodies in the world, demonstrating a pronounced north-south salinity gradient from fully marine- to almost freshwater conditions in the northern parts (Voipio 1981; HELCOM 2018). Due to shipping and man-made waterways, the Baltic Sea contains 173 recorded NIS, many of which display self-sustaining populations (Leppäkoski et al. 2002; Ojaveer et al. 2010, 2017; Reusch et al. 2018; ICES 2022a) and whose introduction events have become more pronounced in recent decades (HELCOM 2023). The susceptibility of the Baltic Sea to the introduction and establishment of NIS is likely due to a combination of anthropogenic disturbances (e.g. eutrophication, pollution, intensive fishing and climate change), as well as the naturally low biodiversity and its brackish water conditions, allowing NIS of both marine and limnetic origin to settle and establish (Paavola et al. 2005; Ojaveer et al. 2010; Olenin et al. 2017; Reusch et al. 2018).

The round goby (*Neogobius melanostomus*), originally from the Ponto-Caspian area, is one of the most widespread invasive fish species in the Northern Hemisphere (Kornis et al. 2012; ICES 2022b). In the Baltic Sea, it was first detected in the Gulf of Gdansk in 1990 (Skóra and Stolarski 1993) and has since then established and spread in most coastal zones of the region (ICES 2022b), where secondary spread has likely been aided by shipping (Azour et al. 2015; Kotta et al. 2016). The invasion success of this species has been manifested by rapid population growth in recent years (Kruze et al. 2023), with densities occasionally reaching 20 individuals/m^2 (Puntila-Dodd et al. 2018). Round goby feeds on a wide range of prey (Schwartzbach et al. 2020; van Deurs et al. 2021; Wallin-Kihlberg et al. 2023), displays aggressive behaviour (Dubs and Corkum 1996, Balshine et al. 2005, Ericsson et al. 2021), is tolerant to a wide range of temperatures and salinities (Behrens et al. 2017, 2022; Christensen et al. 2021) and has a high reproductive turnover rate (Jude 1997). Although the overall impacts of its establishment are deemed ecosystem- and context-specific (Hirsch et al. 2016), it has been shown to decimate local invertebrate populations (van Deurs et al. 2021; Nõomaa et al. 2022), compete with native species for prey (Karlson et al. 2007; Skabeikis et al. 2019; Ericsson et al. 2021) and create new energetic pathways (Almqvist et al. 2010). Thus, the impacts of round goby on Baltic Sea food webs and habitats are pronounced and multifaceted, yet our knowledge regarding the underlying assembly mechanisms and processes determining its establishment is still limited.

Trait-based approaches provide a mechanistic way to address key aspects of biological invasions (Violle et al. 2007; Belmaker et al. 2013; Quell et al. 2021 Steger et al. 2022 Vivó-Pons et al. 2023). This is because traits of NIS may highlight potential interactions and niche overlap with native species and also contribute to the understanding of community assembly processes determining NIS establishment. In this study, we use a trait-based approach to investigate the degree of niche overlap and functional distinctiveness of round goby relative to native fish species in the recipient communities using the Baltic Sea as a case study. We aimed to address the following questions: i) Is round goby functionally distinct or similar compared to the regional pool of native species? ii) Which traits make round goby more or less distinct? iii) To what extent is the distinctiveness of round goby at the local scale influenced by abiotic and biotic factors?

Materials and methods

Data collection

Monitoring data of coastal fish communities where round goby is present was obtained from the Swedish national and regional coastal fish monitoring programme as registered in the national coastal fish database - KUL (https://www.slu.se/kul). The data were extracted for 14 locations sampled between 2008–2021, covering from the south-western Baltic Sea (Stavstensudde) to the Bothnian Sea (Gävlebukten; Fig. 1). Two gear types, Nordic coastal multi-mesh monitoring gillnets and sets of nets, were used in the selected monitoring locations. The Nordic nets consist of nine panels of different mesh-sizes (10, 12, 15, 19, 24, 30, 38, 48 and 60 mm centre knot-to-centre knot), are 1.8 m deep and 50 m long. The sets of nets consist of a number of linked mono-mesh gillnets with mesh sizes between 21–60 mm centre knot-to-centre knot (HELCOM 2019). In Mönsteras, Simpevarp, Muskö and Vinö, between four and six stations were fished over three to six nights within the same week every year with the sets of nets. In the rest of the monitoring locations, between 35 and 50 fixed stations were fished with Nordic nets during one night per year, within the same week every year. Those stations are distributed according to depth-stratified design covering 0–3, 3–6, 6–10 and 10–

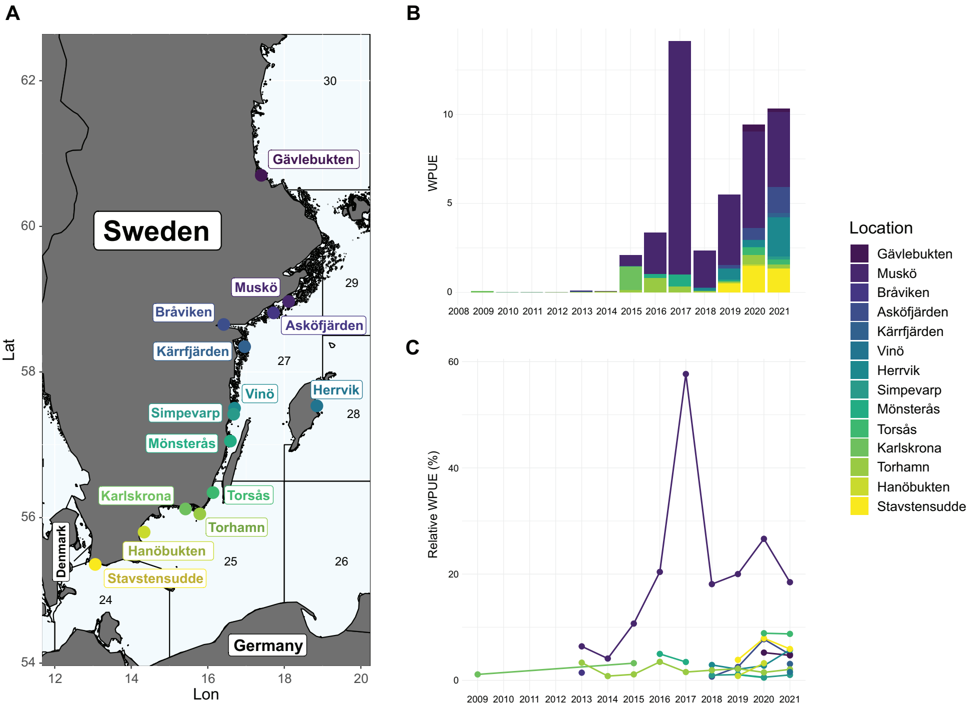

Figure 1. Map of the study area including positions of all sampled locations (**A**). WPUE of round goby for each year and sampling location (**B**). Mean relative WPUE of round goby per year at each location (**C**).

20 m depths (HELCOM 2019). Both types of gears used are set at the bottom of the coastal area. All catches were registered as numbers of individuals per species per length class (1 cm). Thereafter, the total weight per species (g) was transformed into weight per unit effort (WPUE). As not all fish were weighed during the monitoring, weight-length relationships were used to estimate the species weight if missing. It is important to note that the gears used are not the most optimal to catch round gobies or other demersal species with a more sedentary behaviour. Hence, the derived relative biomass (WPUE) of round goby compared to the native species is likely underestimated. To avoid inclusion of sporadically occurring species, we only included those species representing 99.5% of the total species occurrences in the data, resulting in a total of 27 species. We separated the total initial weight identified as *Platichthys flesus* in our data, based on observed proportions between *P. flesus* and *P. solemdali*, a recently discovered cryptic species of flounder (Momigliano et al. 2018; Florin et. al. unpublished data).

Trait data collection

In order to represent the general ecology of the species, a total of 11 categorical traits were selected, with 37 different trait modalities: habitat switching, parental care, territorial behaviour, diet, temperature preference, development mode, pharyngeal bones, habitat, fin type, body type and length class (Table 1). The classification and selection of traits builds on previous trait-based descriptions of marine organisms aiming to represent their behaviour, feeding, reproductive or survival strategies (Litchman and Klausmeier 2008; Törnroos and Bonsdorff 2012; Litchman et al. 2013). Similar criteria for trait selection have been adopted in recent studies of marine fish community structure and changes (e.g. Dencker et al. (2017); Pecuchet et al. (2017); Beukhof et al. (2019a, 2019b)). Trait information was obtained from online trait data portals like FishBase (https://www.fishbase.org.au/v4), scientific and grey literature and, when needed, supplemented by expert knowledge, following the same procedure as in Törnroos et al. (2015, 2019). Traits where species display a single modality (e.g. territorial behaviour, fin type, body type) were treated as categorical. For multi-choice nominal traits, where species can display multiple modalities (e.g. diet), each modality was scored between 0 and 1 representing the probability of being displayed by a given species (Suppl. material 1: table S1). For example, a species feeding mainly on benthic prey, but that occasionally feeds on other fishes, could receive a score of 0.8 for the modality “benthivorous” and 0.2 for the modality “piscivorous”. Otherwise, if a species feeds equally on benthic and fish prey, it would be scored 0.5 for each modality.

Functional distinctiveness between round goby and native species

To assess the degree of (trait) niche overlap between round goby and native species, we used the functional distinctiveness index (D), weighted by species biomass. The functional distinctiveness index is defined as the mean functional distance of a single species to all other species present in a given community (Violle et al. 2017):

$$D_i = \frac{\sum_{j=1;j\neq i}^{N} d_{ij}\, x\, Ab_j}{\sum_{j=1;j\neq i}^{N} Ab_j} \qquad \text{(Equation I)}$$

where d_{ij} is the functional distance between species i and j, N accounts for the number of species in the community and Ab_j accounts for the relative importance (i.e. relative WPUE) of species j. A high D value indicates that a species is functionally distinct compared to the other species in the community (Violle et al. 2017).

We computed the functional distance between each pair of species (d_{ij}) given by Gower's general coefficient of similarity (Gower 1971). This dissimilarity metric represents functional distances by giving equal weights between traits coded in different format (i.e. numerical, categorical or ordinal; Pavoine et al. (2009)). We are aware that mixing continuous with categorical, dummy or fuzzy-coded traits could result in a bias in the computed dissimilarities, due to an unbalanced contribution of traits coded in non-continuous formats (de Bello et al. 2021). However, in our analysis, we do not have any continuous traits (Table 1; Suppl. material 1: table S2) and, therefore, this potential issue is not directly applicable to our study. In any case, to avoid bias due to one or a few traits having a disproportional effect on D, we used an integrated process testing for multiple combinations of traits to compute the functional distances between species, obtaining a single distances matrix for each possible combination of traits (Coulon et al. 2023; Vivó-Pons et al. 2023). The resulting matrices obtained from all the possible trait combinations were summarised into a mean functional distance matrix for each pair of species present in the regional pool. From this overall mean functional distances matrix, we computed functional distinctiveness for all species, including round goby, both at a regional and local spatial scale with the corresponding regional or the different local species pools. To weight distinctiveness at a regional scale we obtained a unique value representing the overall relative WPUE of each species from 2009 to 2021, in order to cover the whole invasion process of round goby from the initial occurrence in the region to its subsequent spread. At a local scale, round goby's distinctiveness was weighted using the exact relative WPUE at each unique sampling event, i.e. within each sampled community. The functional distances were computed with the function "compute_dist_matrix" from the "funrar" package (Grenié et al. 2017) in R software, version 4.1.0 (R Core Team 2021).

In order to investigate if round goby was more or less distinct than the other species in the regional pool, we compared the value of functional distinctiveness of round goby relative to the values for all native species in the data set. Furthermore, to assess and compare the degree of niche overlap in trait space between round goby and the native species, we performed a Principal Coordinate Analysis (PCoA) on the overall pairwise dissimilarity matrix for the regional species pool (Belmaker et al. 2013; Vivó-Pons et al. 2023). Subsequently, we classified the species as dissimilar or similar, based on their distinctiveness value by grouping them into quartiles. The first quartile accounted for the functionally common species, while the fourth quartile accounts for the most functionally distinct species with higher values of distinctiveness.

Table 1. List of included traits and modalities, the number and percentage of species displaying each modality and the explanation of each modality. Modalities in bold are displayed by round goby.

Traits	Nature of the trait	Categories (n = 37)	N species having that category	Frequency (% of species having that category)	Explanation
Diet	Multichoice nominal	**Benthivorous**	18	46.22	Feeding mainly on benthic invertebrates as adults
		Planktivorous	7	16.59	Feeding mainly on plankton as adults
		Generalist	7	21.59	Feeding on the other categories as well as on detritus, algae etc. as adults
		Piscivorous	8	15.56	Feeding mainly on fishes as adults
Habitat	Categorical	**Demersal**	16	59.26	Living and feeding on or near the bottom as adults
		Benthopelagic	7	25.93	Living and feeding near the bottom as well as in mid-waters or near the surface as adults
		Pelagic	4	14.81	Living and feeding in the open water throughout ontogeny
Fin type	Categorical	Emarginated	5	18.52	Caudal fin with a rather sharp and straight end with an indent in the middle
		Forked	12	44.44	Caudal fin with the indent deeper than in emarginated fins
		Absent	1	3.70	
		Rounded	8	29.63	Caudal fin evenly rounded and convex
		Truncated	1	3.70	Caudal fin with a rather sharp edge that can be flat, square or straight
Body type	Categorical	Deep	6	22.22	Body is compressed from the sides
		Elongated	8	29.63	Body is rather long and slender
		Flat	2	7.41	Body is flat (depressed) with eyes on the same side
		Normal	11	40.74	Body is proportional and neither compressed nor depressed
Development mode	Categorical	Scattered	4	14.81	Eggs are scattered on the bottom
		Viviparous	1	3.70	Eggs receive nourishment from the female during development and hatch inside the body of the female
		Ovoviviparous	1	3.70	Eggs do not receive nourishment from the female during development
		Pelagic	2	7.41	Eggs float freely in the water column
		Adherent	17	62.96	Eggs adhere to a substrate in a layer
		Mass clump	2	7.41	Eggs adhere to each other, forming a clump
Length class (maximum length according to FishBase)	Ordinal	0–10 cm	2	7.41	
		10–20 cm	11	40.74	
		21–30 cm	7	25.93	
		31–40 cm	2	7.41	
		41–50 cm	5	18.52	

Traits	Nature of the trait	Categories (n = 37)	N species having that category	Frequency (% of species having that category)	Explanation
Temperature preference	Categorical	Cold	9	33.33	
		Warm	18	66.67	
Territorial behaviour	Categorical	**Yes**	8	29.63	The species holds and defends a territory or has a very narrow home range, usually related to spawning, but not necessarily
		No	19	70.37	
Parental care	Categorical	**Yes**	8	29.63	The species exhibits some sort of parental care, for example, carries or guards the eggs/young
		No	19	70.37	
Habitat switching	Categorical	**Yes**	21	77.78	The species switches habitat due to spawning, feeding migration or winter migration
		No	6	22.22	
Pharyngeal bones	Categorical	**Yes**	16	59.26	The species has pharyngeal bones or branchial tooth plates
		No	11	40.74	

Key traits affecting distinctiveness

To assess the effect and relative importance of each trait on functional distinctiveness, we calculated the difference between the distinctiveness values for each species based on all traits (Di, T) and the values when each individual trait was removed from the analysis (Di, T-t). We then divided the difference by regional distinctiveness, including all traits (Di, T) as follows:

$$Effect\ of\ trait_t\ on\ D_i = \frac{D_{i,T} - D_{i,T-t}}{D_{i,T}} \times 100 \qquad \text{(Equation II)}$$

Drivers of round goby functional distinctiveness

In order to reflect the key environmental conditions affecting the local distinctiveness of round goby at each sampling site, we compiled data of bottom salinity, temperature and depth, measured in situ as part of the fish monitoring programme. For some locations, bottom salinity and temperature data were incomplete, hence we complemented the monitoring programme data with data derived from the ice-ocean model NEMO-Nordic (based on NEMO-3.6, Nucleus for European Modelling of the Ocean; https://doi.org/10.48670/moi-00013) from Copernicus Marine Service (https://marine.copernicus.eu/). Before completing the available in-situ data with model-derived data, we compared values of available environmental variables derived from both sources. This sensitivity test showed a high correlation for both bottom temperature (r = 0.75) and salinity (r = 0.77) (Suppl. material 1: fig. S1). Therefore, we decided to use both in-situ data and modelled data for sampling events lacking such information. In addition, we also obtained the model derived data on dissolved oxygen and chlorophyll a for each location at the corresponding sampling date. We used distance to the open sea as a proxy for coastal exposure, extracted by using the "cost distance" function in ArcGIS Pro (see Erlandsson et al. (2021) for details). Then, to estimate the effect of biotic drivers acting on local distinctiveness we further estimated species richness and evenness per location, based on WPUE. All variables had a variance inflation factor of < 2, indicating a lack of multicollinearity between predictors.

To determine how the local functional distinctiveness of round goby was affected by the selected environmental and biotic variables at each sampling event, we applied a multi-model approach using both Generalised Additive Mixed Models (GAMMs) and Random Forests (RFs). This allows for comparison of the derived response curves and variable importance to assess robustness and sensitivity of results to model choice (Lindegren et al. 2020, 2022). For the GAMM, we applied the following model:

$$\mathit{Round\ goby\ D}_{l,t} = a + s(\mathit{Bottom\ oxygen}_{l,t}) + s(\mathit{Bottom\ salinity}_{l,t}) + s(\mathit{Bottom\ temperature}_{l,t}) + s(\mathit{Depth}_{l,t}) + s(\mathit{Chlorophyll}_{l,t}) + s(\mathit{Exposure}_{l,t}) + s(\mathit{Richness}_{l,t}) + s(\mathit{Evenness}_{l,t}) + d(\mathit{Location\ x\ Time\ step}) + e(\mathit{Gear}) + \epsilon$$

where the response variable *D* is the distinctiveness for the round goby at each sampling location *l* at a specific time *t*. The parameter *a* is the intercept, *s* is the thin plate smooth function for each of the covariates and ϵ the error term. To account for the potential effect of repeating measures within the same area, we also included a random effect *d* for each sampled location at a certain time (i.e. "Location × Time step" in the formula). The inclusion of this random effect in the model served to account for possible variation in distinctiveness between locations due to their different stages of invasion. Finally, *e* accounts for the random effects of the different gears used during the sampling. The degrees of freedom of the spline smoother function (*s*) were constrained to three knots ($k = 3$) to allow for non-linearities, but restricting its flexibility on the model fitting. Since *D* ranges between 0 and 1, the model was fitted with a beta-regression distribution (Ferrari and Cribari-Neto 2004).

Random forest (RF) is a machine-learning tool comprising ensembles of decision trees that rely on bootstrap aggregation (Breiman 2001). It is capable of producing complex non-linear shapes in single and multiple dimensions, while accounting for interaction amongst all predictors. Random subsets of the data are selected to train individual classification trees within the random forest, whilst the final forest prediction is obtained by averaging predictions across all individual trees. The same response and explanatory variables were used as in the GAMM formulation above. Here, we used the final RF to estimate the relative importance of each predictor (based on 1000 individual trees) to compare it with the importance estimated with GAMMs. In addition, we applied RF to visualise the partial response curves of each explanatory variable.

To evaluate the predictive accuracy of the fitted models between methods, we also performed a formal cross-validation analysis by fitting the same model with a randomly sampled subset of the data (75% of the total observations) and predicting round goby distinctiveness with the remaining 25% of observations that were not used to fit the models. The cross-validation was repeated 100 times, selecting a new random subset of observations in each iteration for model training and testing. Subsequently, we assessed the range of uncertainty of the predictions (i.e. mean squared error) and the range of explained variance for both methods. All statistical analyses were conducted using the R software, version 4.1.0 (R Core Team 2021) and using the package "mgcv" (Wood 2017) and "randomForest" (Liaw and Wiener 2002).

Results

Functional relationship between round goby and natives

Amongst all species, Eurasian perch (*Perca fluviatilis*) was the most abundant taxa in the monitoring data in terms of weight, representing 24% of the total biomass, followed by common roach (*Rutilus rutilus*; 14.8%) and Atlantic cod (*Gadhus morhua*; 8.3%), while round goby represented only 1.04% of the total biomass (Suppl. material 1: table S3). The estimated functional distinctiveness values (*D*) for the regional species pool ranged from 0.33 (*Gymnocephalus cernuus*) to 0.62 (*Nerophis ophidion*). Round goby had a distinctiveness value of 0.49, which is slightly higher than the median *D* of the fish community (0.44; Fig. 2). This makes round goby the ninth most distinct

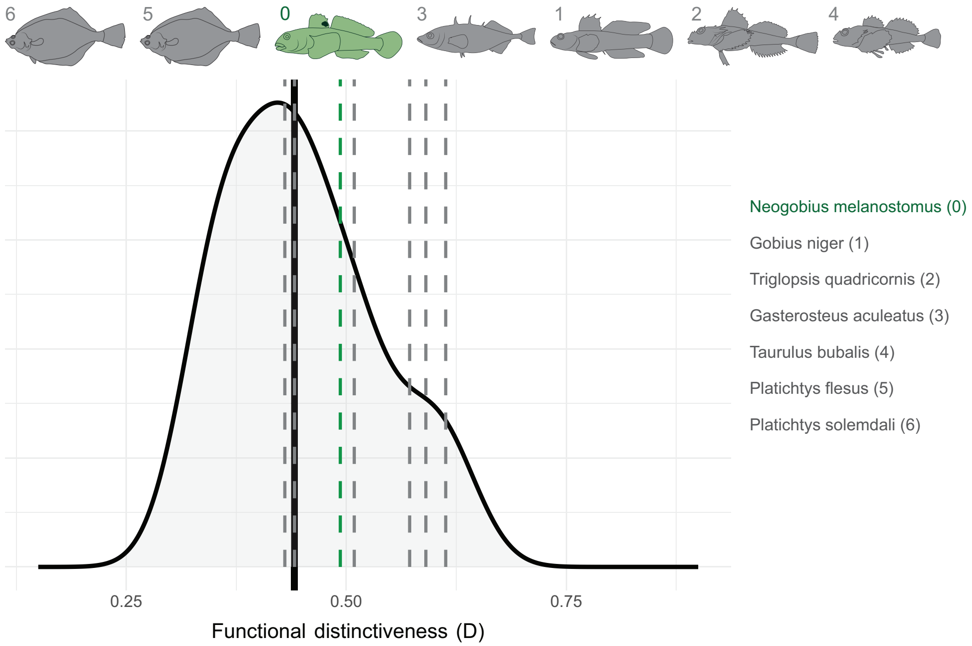

Figure 2. Position of round goby and its six most functionally similar species along the distribution of WPUE-weighted distinctiveness values from the regional species pool. The black vertical line indicates the median value of distinctiveness for the whole community. The highlighted species are ordered according to their values of distinctiveness. The numbers on top of them only indicate the corresponding names.

species out of all 27 species in the dataset. However, round goby was less distinct than four of the six species to which it is most functionally similar (Fig. 2; Suppl. material 1: table S3).

The first two axes of the PCoA of functional distances (trait space) explained 35.1% and 23.2% of the total variability between species, respectively. Round goby was located closer to the most functionally distinct species (defined by the 4th quartile) in the trait space (Fig. 3A). Functionally distinct species were generally defined by displaying some of the following trait modalities: being demersal, strictly benthivorous with rounded fins, having pharyngeal bones, laying eggs in clumps, displaying territorial behaviour and parental care or with no capacity of habitat switching (Fig. 3B, C). In contrast, the most functionally common species (defined by the first quartile) were mostly defined by showing a strictly generalist diet, laying adherent eggs, having forked fins and displaying neither parental care nor showing territorial behaviour (Fig. 3B, C).

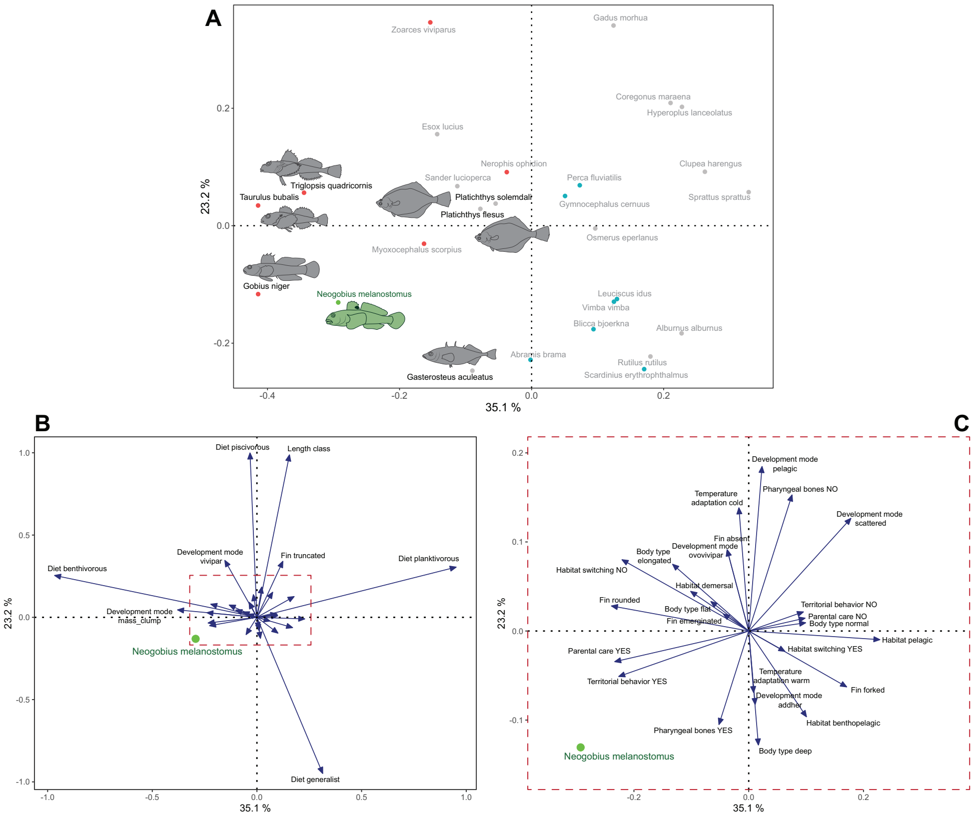

Figure 3. Community trait space given by a PCOA of functional distances between all species (**A**). The green dot and drawing indicate the position of round goby. Red dots indicate the position of species classified as being the most distinct, while blue dots define species classified as most similar compared to the rest of the community. Names in bold indicate the position of the most functionally similar species to round goby **B** biplot of trait vectors and loadings showing which traits are influencing the position of each species in the PCOA **C** zoom of the central part of the biplot.

Key traits affecting round goby distinctiveness

Amongst the set of traits considered, displaying parental care had the highest influence on round goby distinctiveness, with a relative increase of 7.33% in *D* values when including this trait. This positive effect of parental care was closely followed by having an elongated body type (7.26%), a rounded fin (6.61%) and territorial behaviour (6.40%; Fig. 4). Having a benthivorous diet showed the most negative effect on round goby distinctiveness (-10.28%; Fig. 4), indicating that this trait modality is shared by many species and make round goby less distinct compared to the native community.

The influence of each trait on the whole fish community distinctiveness demonstrated that body shape and fin type had the highest median positive effect (5% and 4.73%), while diet showed the most negative effect (-6.86%; Fig. 4). The positive effects of parental care and territorial behaviour on round goby distinctiveness stand out when compared with the other species, as the median overall effect for these two traits was negative amongst the native species (-6.47% and -5.15%, respectively).

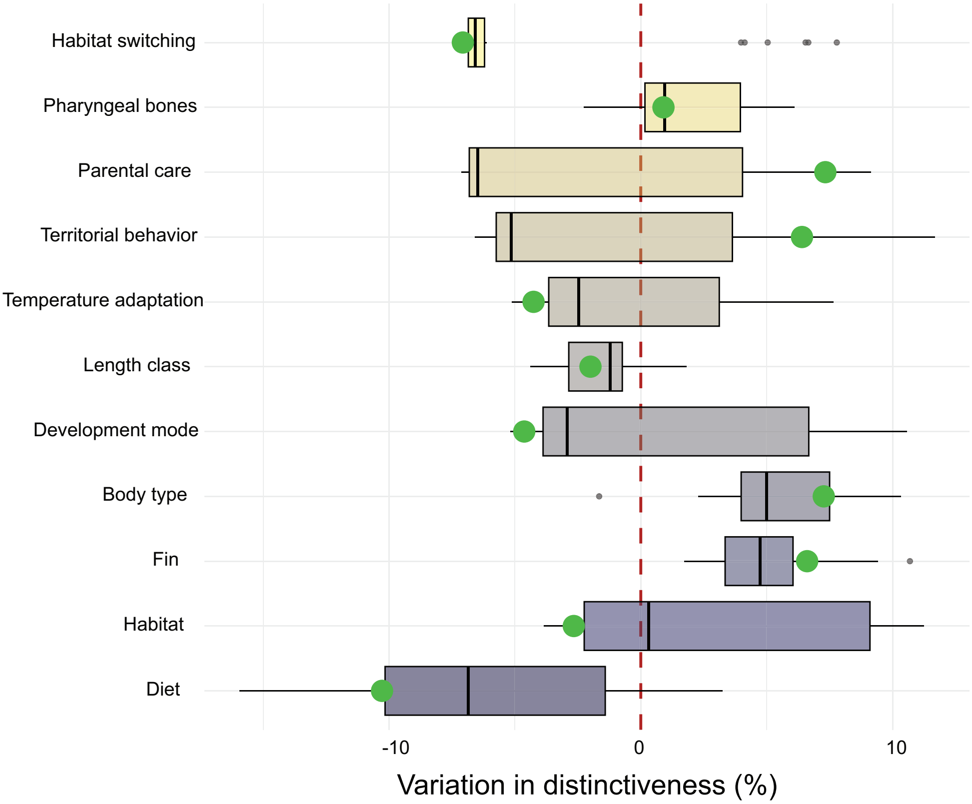

Figure 4. Effect of traits on species functional distinctiveness, shown as the percentage change in overall distinctiveness if excluding each individual trait in the calculations. Results are shown when using either the whole species pool with the green dots representing the effect of each trait on round goby functional distinctiveness.

These values rank round goby as the 2nd species in the regional pool with the highest increase in distinctiveness when including parental care and the 4th when including territorial behaviour.

Spatial patterns and drivers of round goby distinctiveness

Distinctiveness values for round goby at each location were highly variable, with the highest mean value found in Hanöbukten (0.64) and the lowest mean distinctiveness in Hervik (0.44). In 7 out of 14 locations, the mean distinctiveness of round goby was higher than the overall value when compared to the regional fish community (Fig. 5A). Regarding the change in distinctiveness over time, some variation between and within locations was observed; however, no major changes within locations were detected (Fig. 5B).

From the selected set of potential abiotic and biotic drivers, species richness and evenness, depth, coastal exposure, bottom temperature and oxygen showed significant effects on round goby distinctiveness in the fitted GAMM (Table 2). The relative importance of predictors was similar across across GAMM and RF, showing only slight differences in the order and position of the most important variables (Suppl. material 1: table S4). The partial response curves were also highly similar across methods (Fig. 6). Both species richness and evenness demonstrated a negative non-linear relationship with round goby local distinctiveness (Fig. 6A, B). For species richness, the relationship displayed a U-shaped curve in the GAMM, probably due to the lack of observations from very species rich areas, but a more marked non-linear decrease in the RFs (Fig. 6B). In the case of species evenness, the relationship was dome-shaped, more clearly depicted in the GAMM (Fig. 6A), with the highest distinctiveness observed at evenness values of ~ 0.5. For the abiotic variables, bottom temperature and coastal exposure also showed dome-shaped relationships, with the highest values of round goby distinctiveness found in moderately exposed areas at temperatures ranging from ~ 7.5 to 12.5 °C (Fig. 6D, F). Although the relationship with bottom oxygen was also

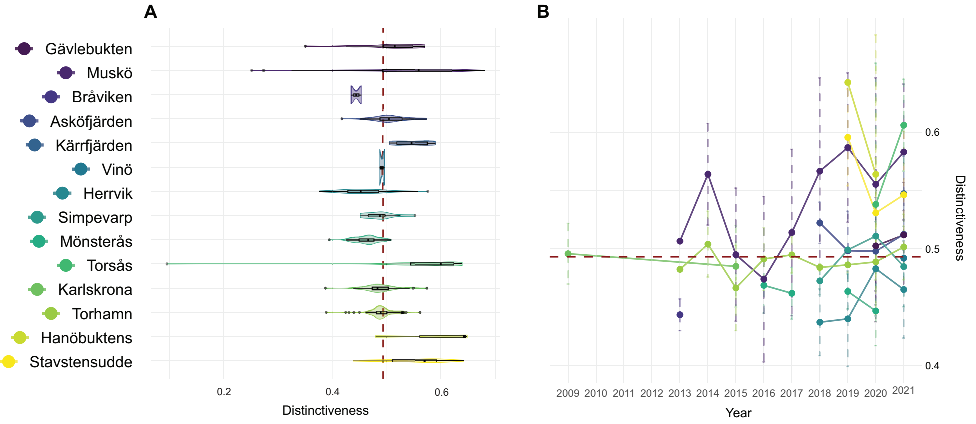

Figure 5. Distribution of round goby local distinctiveness at each sampling site (**A**) and over time (**B**).

Table 2. Results of the GAMM models for round goby local functional distinctiveness. Edf refers to estimated degrees of freedom; significant effects are highlighted in black.

Variables	edf	Chi squared	p-value	R squared	Deviance explained	N	
Eveness	1.803	9.768	**0.015**				*
Richness	1.923	25.361	**< 0.001**				***
Depth	1.001	7.621	**0.006**				**
Bottom temperature	1.906	18.323	**< 0.001**				***
Bottom salinity	1.000	0.370	0.543				
Bottom oxygen	1.000	4.994	**0.025**				*
Chlorophyll	1.004	0.918	0.342				
Exposure	1.927	22.167	**< 0.001**				***
Location x Time step (1st)	1.331	2.314	0.205				
Location x Time step (2nd)	1.812	15.147	**0.017**				*
Location x Time step (3rd)	9.695	198.967	**< 0.001**				***
Gear	0.889	93.769	**< 0.001**				***
				0.498	51.7%	762	

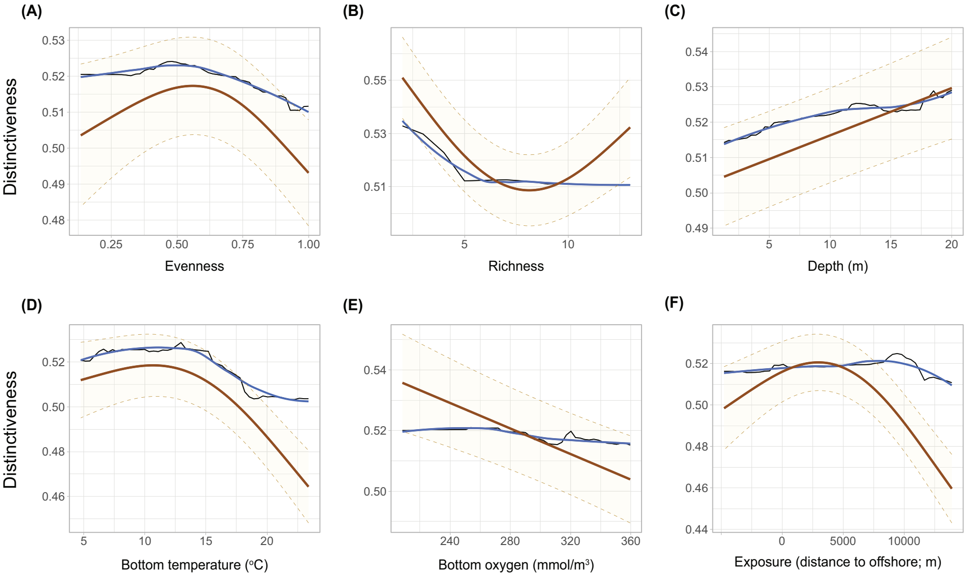

Figure 6. Partial effect curves derived from the models fitted with both GAMM and Random Forest. Only the variables that had a significant effect in GAMMs are shown. The yellow line and ribbon represent the partial curve and the standard deviation derived from the GAMM. The blue and black lines represent the partial effect curve and the corresponding variability derived from the Random Forest.

negative, the trend was linear in the GAMM and dome-shaped for RF, with the highest local distinctiveness values around ~ 220 to 260 mmol/m^3 (Fig. 6E). Conversely, depth showed a positive linear relationship with round goby's local distinctiveness in the GAMM and a positive non-linear relationship in RF (Fig. 6C).

Finally, both methods showed similar values of explained variance (i.e. 51.7% for GAMM and 53.8% for RF). The cross-validation analysis demonstrated a better overall performance for RF, illustrated by lower mean squared error of predicted round goby distinctiveness compared to observation not used for model training (Suppl. material 1: fig. S2).

Discussion

The degree to which NIS display similar or dissimilar traits compared to native species of recipient communities is debated largely due to contrasting results from available studies, primarily conducted in terrestrial ecosystems (Cleland 2011; Escoriza and Ruhí 2016; Xu et al. 2022). Consequently, a better understanding of the trait (niche) overlap amongst native species and NIS, as well as the underlying assembly processes that determine their establishment is needed (Gallien et al. 2014; Gallien and Carboni 2017), especially in marine environments. Our trait-based study focusing on round goby, one of the most widespread invasive fish species in the Northern Hemisphere (Kornis et al. 2012; ICES 2022b) demonstrated that this non-native fish is not particularly distinct in terms of its overall trait composition compared to the native species pool of the Baltic Sea coastal fish community. Although occupying a seemingly isolated position in the community trait space, it does share combination of traits with several other ecologically similar native species, such as black goby (*Gobius niger*), longspined bullhead (*Taurulus bubalis*) and fourhorn sculpin (*Triglopsis quadricornis*).

Although round goby is not generally different from the regional pool of native species in terms of its overall trait composition, we observed notable differences in terms of individual trait modalities, primarily by display of territorial behaviour and parental care. This indicates that native species generally display a reproductive strategy that does not involve defending a territory, nor protecting their offspring. More specifically, round goby males display several types of parental care, including egg inspection, ventilation and nest guarding (Kornis et al. 2012). Egg inspection and ventilation are beneficial for egg survival as they can limit the spread of diseases within the nest, prevent accumulation of sediment and increase the flow of oxygenated water over the eggs (Jones and Reynolds 1999; Meunier et al. 2009). Males can show different types of aggressive behaviour when guarding the nest, such as strength displays, attacking intruders or chasing away potential predators (Wickett and Corkum 1998; Meunier et al. 2009). The expression of male parental care is strongly related to territoriality, especially in sequentially polygynous spawners (mating with multiple females), like round goby (Ah-King et al. 2005). No offspring need to be present to spark aggressive behaviour, as the males can act in a similar way when they defend their territory or shelter from other fishes (Dubs and Corkum 1996; Balshine et al. 2005). Displaying aggression can provide an adaptive advantages, for example, in the protection of offspring or competition for resources, potentially increasing the invasion success of NIS (Chapple et al. 2012). In terms of offspring protection, less aggressive fishes could be easily expelled in a nest intrusion situation (Dubs and Corkum 1996; Balshine et al. 2005). Aggressive territorial defence could also help round goby in securing and protecting good feeding grounds (Karlson et al. 2007) or even deter potential predators, as being aggressive has been recognised as anti-predator behaviour (Huntingford 1976; Hess et al. 2016). Thus, it is possible that the display of territorial behaviour and parental care by round goby could partly explain its invasion success in the Baltic Sea (Christensen et al. 2021; Puntila-Dodd et al. 2021; Backström and Winkelmann 2022; Behrens et al. 2022). Our findings support the idea that NIS might be successfully established by only differing from natives in terms of one or a few traits, allowing them to cope with existing environmental conditions while, at the same time, colonise more specific or partly vacant niches (Cleland 2011; Gallien et al. 2014; Cadotte et al. 2018; El-Barougy et al. 2020).

While generally similar to native species at the regional scale, our study demonstrates pronounced spatio-temporal variation in terms of local distinctiveness of round goby between and within sampling locations over time. The wide range of values (i.e. from < 0.2 to > 0.6) indicates that round goby can locally co-exist with native species that are either functionally similar or different to itself, reflecting its broad environmental tolerance (Behrens et al. 2017, 2022; Christensen et al. 2021). In terms of the environmental drivers potentially explaining the variation in local distinctiveness, both our methods indicate that round goby appears to be more distinct in colder and deeper monitoring locations with low oxygen and an intermediate level of exposure. These areas are typically inhabited during the winter months following a seasonal offshore-onshore migration (Behrens et al. 2022). The colder, offshore areas in the Baltic Sea are primarily dominated by more marine species, such as Atlantic cod, herring (*Clupea harengus*), sprat (*Sprattus sprattus*) or eelpout (*Zoarces viviparus*) (Olsson et al. 2012; HELCOM 2018; Olsson 2019). These species are generally dissimilar compared to round goby, as they are located almost in an opposite position in the community trait space. In contrast, round goby is functionally more similar to native species in the warmer, shallow and less exposed monitoring locations that are mainly occupied by, for instance, European perch, several species of cyprinids, sticklebacks (Gasterosteidae) and other gobies (Gobiidae) (Olsson et al. 2012; HELCOM 2018). Notably, the three-spined stickleback (*Gasterosteus aculeatus*) and black goby (*Gobius niger*) are two of the six most functionally similar species to round goby, with black goby having fairly similar ecology and habitat requirements (Matern et al. 2021).

The ability to colonise a broad range of habitats and therefore co-exist with different pools of native species with different trait composition may help explain the derived relationships with the biotic variables included in our statistical analysis. For instance, the negative effect of species richness likely reflects the higher local distinctiveness of round goby when co-occurring with the fewer and functionally more dissimilar marine species from colder and deeper locations. Contrarily, when found together with the more species from the native community at more shallow and warmer locations, the likelihood of round goby co-occurring with more functionally similar species is higher, thus explaining its lower local level of distinctiveness at higher richness. This is likely facilitated also by the strong relationship between species and functional richness in the Baltic Sea region (Törnroos et al. 2015; Pecuchet et al. 2016). In terms of evenness, it is assumed that most ecological niches are occupied when species abundances are evenly distributed (Hillebrand et al. 2008). Conversely, highly uneven communities tend to be dominated by the best performers under local environmental conditions that can outcompete functionally-similar species (Hillebrand et al. 2008). The highest local distinctiveness of round goby at low to moderate evenness may indicate a situation where round goby needs to both display similar traits to be able to adapt to the local environment (i.e. environmental filtering), but also being dissimilar (i.e. in this case, territoriality and parental care) relative to the most dominant native species in order to avoid competitive exclusion (Gallien et al. 2014).

In summary, the application of this trait-based approach to the case of round goby in the Baltic Sea shows a partial (trait) niche overlap with native fish species that appears to increase locally when round goby occurs with communities from shallow, inshore and warmer areas. Despite this partial overlap with native species, we also demonstrated that round goby shows pronounced differences compared to the native community in its display of parental care and territorial behaviour. Such differences could play an important underlying role behind round goby's invasion success in the Baltic, as well as in defining the type of interactions with native species. Based on our results, non-aggressive native species that partially share their niche with round goby might be harmed or displaced in the case of direct competition with this NIS for similar resources (e.g. feeding grounds, sheltered areas, nesting sites). Due to the context dependence (i.e. the species and traits selected) of this study, caution should be taken when expanding our conclusions to different scenarios of round goby invasion. For that reason, we encourage the use of similar trait-based approaches, based on functional distinctiveness to further address the invasion of round goby in other areas, with a different environment and species composition (e.g. the North-American Great Lakes or central European rivers). If similar patterns emerge, this would contribute to the understanding of why this species has managed to successfully establish in such different regions, as well as a better understanding if round goby shows similar interactions with native fishes in other areas. Additionally, investigating how round goby dominance could be affected when it co-exists with more similar or dissimilar native species in local communities could also be valuable to define the niche or conditions that this species needs to become invasive (Blackburn et al. 2011). Such an approach could potentially be used to assess the sensitivity of particular areas to the invasion and address potential impacts of round goby on other native fishes (e.g. displacement, competition, facilitation), by combining its environmental preferences with the type of community where round goby appears to be more dominant. Our results and their potential applications may, therefore, be highly relevant if integrated within existing risk assessment tools for biological invasions (Lodge et al. 2016) in order to prioritise and enhance management and conservation actions towards the round goby.

Acknowledgements

We wish to thank the Swedish Agency for Marine and Water Management and OKG Aktiebolag for funding the regional and national monitoring programmes together with all the people involved who sorted, identified and measured the included species in the database, ensuring the access and availability to high-quality time-series data. In addition, we would like to thank all the reviewers involved in the revision process of this work, as all the comments and feedback provided helped to improve the quality of this manuscript. A.V.P and M.L. acknowledge financial support from the European Union's Horizon 2020 projects "Mission Atlantic" (ID: 862428) and "B-USEFUL" (ID: 101059823).

References

Ah-King M, Kvarnemo C, Tullberg BS (2005) The influence of territoriality and mating system on the evolution of male care: A phylogenetic study on fish. Journal of Evolutionary Biology 18(2): 371–382. https://doi.org/10.1111/j.1420-9101.2004.00823.x

Almqvist G, Strandmark AK, Appelberg M (2010) Has the invasive round goby caused new links in Baltic food webs? Environmental Biology of Fishes 89(1): 79–93. https://doi.org/10.1007/s10641-010-9692-z

Anton A, Geraldi NR, Lovelock CE, Apostolaki ET, Bennett S, Cebrian J, Krause-Jensen D, Marbà N, Martinetto P, Pandolfi JM, Santana-Garcon J, Duarte CM (2019) Global ecological impacts of marine exotic species. Nature Ecology & Evolution 3(5): 787–800. https://doi.org/10.1038/s41559-019-0851-0

Azour F, van Deurs M, Behrens J, Carl H, Hüssy K, Greisen K, Ebert R, Møller P (2015) Invasion rate and population characteristics of the round goby *Neogobius melanostomus*: Effects of density and invasion history. Aquatic Biology 24(1): 41–52. https://doi.org/10.3354/ab00634

Backström T, Winkelmann C (2022) Invasive round goby shows higher sensitivity to salinization than native European perch. NeoBiota 75: 23–38. https://doi.org/10.3897/neobiota.75.86528

Balshine S, Verma A, Chant V, Theysmeyer T (2005) Competitive Interactions between Round Gobies and Logperch. Journal of Great Lakes Research 31(1): 68–77. https://doi.org/10.1016/S0380-1330(05)70238-0

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: A threat to global biodiversity. Marine Policy 27(4): 313–323. https://doi.org/10.1016/S0308-597X(03)00041-1

Behrens JW, van Deurs M, Christensen EAF (2017) Evaluating dispersal potential of an invasive fish by the use of aerobic scope and osmoregulation capacity. PLoS ONE 12(4): e0176038. https://doi.org/10.1371/journal.pone.0176038

Behrens JW, Ryberg MP, Einberg H, Eschbaum R, Florin A-B, Grygiel W, Herrmann JP, Huwer B, Hüssy K, Knospina E, Nõomaa K, Oesterwind D, Polte P, Smoliński S, Ustups D, van Deurs M, Ojaveer H (2022) Seasonal depth distribution and thermal experience of the non-indigenous round goby *Neogobius melanostomus* in the Baltic Sea: Implications to key trophic relations. Biological Invasions 24(2): 527–541. https://doi.org/10.1007/s10530-021-02662-w

Belmaker J, Parravicini V, Kulbicki M (2013) Ecological traits and environmental affinity explain Red Sea fish introduction into the Mediterranean. Global Change Biology 19(5): 1373–1382. https://doi.org/10.1111/gcb.12132 de Bello F, Botta-Dukát Z, Lepš J, Fibich P (2021) Towards a more balanced combination of multiple traits when computing functional differences between species. Methods in Ecology and Evolution 12: 443–448. https://doi.org/10.1111/2041-210X.13537

Beukhof E, Dencker TS, Pecuchet L, Lindegren M (2019a) Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. Marine Ecology Progress Series 610: 205–222. https://doi.org/10.3354/meps12826

Beukhof E, Frelat R, Pecuchet L, Maureaud A, Dencker TS, Sólmundsson J, Punzón A, Primicerio R, Hidalgo M, Möllmann C, Lindegren M (2019b) Marine fish traits follow fast-slow continuum across oceans. Scientific Reports 9(1): 17878. https://doi.org/10.1038/s41598-019-53998-2

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26(7): 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Breiman L (2001) Random Forests. Machine Learning 45: 5–32. https://doi.org/10.1023/A:1010933404324

Cadotte MW, Campbell SE, Li S, Sodhi DS, Mandrak NE (2018) Preadaptation and naturalization of nonnative species: Darwin's two fundamental insights into species invasion. Annual Review of Plant Biology 69(1): 661–684. https://doi.org/10.1146/annurev-arplant-042817-040339

Chapple DG, Simmonds SM, Wong BBM (2012) Can behavioral and personality traits influence the success of unintentional species introductions? Trends in Ecology & Evolution 27(1): 57–64. https://doi.org/10.1016/j.tree.2011.09.010

Christensen EAF, Norin T, Tabak I, van Deurs M, Behrens JW (2021) Effects of temperature on physiological performance and behavioral thermoregulation in an invasive fish, the round goby. Journal of Experimental Biology 224 (1): jeb.237669. https://doi.org/10.1242/jeb.237669

Cleland EE (2011) Trait divergence and the ecosystem impacts of invading species. The New Phytologist 189(3): 649–652. https://doi.org/10.1111/j.1469-8137.2010.03607.x

Coulon N, Lindegren M, Goberville E, Toussaint A, Receveur A, Auber A (2023) Threatened fish species in the Northeast Atlantic are functionally rare. Global Ecology and Biogeography 32(10): 1827–1845. https://doi.org/10.1111/geb.13731

Dencker TS, Pecuchet L, Beukhof E, Richardson K, Payne MR, Lindegren M (2017) Temporal and spatial differences between taxonomic and trait biodiversity in a large marine ecosystem: Causes and consequences. PLoS ONE 12(12): e0189731. https://doi.org/10.1371/journal.pone.0189731

Dubs DOL, Corkum LD (1996) Behavioral Interactions Between Round Gobies (*Neogobius melanostomus*) and Mottled Sculpins (*Cottus bairdi*). Journal of Great Lakes Research 22(4): 838–844. https://doi.org/10.1016/S0380-1330(96)71005-5

El-Barougy RF, Elgamal I, Rohr RP, Probert AF, Khedr AA, Bacher S (2020) Functional similarity and dissimilarity facilitate alien plant invasiveness along biotic and abiotic gradients in an arid protected area. Biological Invasions 22(6): 1997–2016. https://doi.org/10.1007/s10530-020-02235-3

Ericsson P, Persson A, Behrens JW, Brodin T, Hirsch PE, Sundelin A, van Deurs M, von Friesen LW, Nilsson PA (2021) Personality-dependent inter- and intraspecific foraging competition in the invasive round goby, Neogobius melanostomus. Journal of Fish Biology 98(5): 1234–1241. https://doi.org/10.1111/jfb.14652

Erlandsson M, Fredriksson R, Bergström U (2021) Kartering av uppväxtområden för fisk i grunda områden i Östersjön. Aqua reports. https://res.slu.se/id/publ/113831 [April 25, 2023]

Escoriza D, Ruhí A (2016) Functional distance to recipient communities may favour invasiveness: Insights from two invasive frogs. Diversity & Distributions 22(5): 519–533. https://doi.org/10.1111/ddi.12421

Ferrari SLP, Cribari-Neto F (2004) Beta regression for modelling rates and proportions. Journal of Applied Statistics 31(7): 799–815. https://doi.org/10.1080/0266476042000214501

Gallien L, Carboni M (2017) The community ecology of invasive species: Where are we and what's next? Ecography 40(2): 335–352. https://doi.org/10.1111/ecog.02446

Gallien L, Carboni M, Münkemüller T (2014) Identifying the signal of environmental filtering and competition in invasion patterns - a contest of approaches from community ecology. Methods in Ecology and Evolution 5(10): 1002–1011. https://doi.org/10.1111/2041-210X.12257

Gallien L, Mazel F, Lavergne S, Renaud J, Douzet R, Thuiller W (2015) Contrasting the effects of environment, dispersal and biotic interactions to explain the distribution of invasive plants in alpine communities. Biological Invasions 17(5): 1407–1423. https://doi.org/10.1007/s10530-014-0803-1

Geraldi NR, Anton A, Santana-Garcon J, Bennett S, Marbà N, Lovelock CE, Apostolaki ET, Cebrian J, Krause-Jensen D, Martinetto P, Pandolfi JM, Duarte CM (2020) Ecological effects of non-native species in marine ecosystems relate to co-occurring anthropogenic pressures. Global Change Biology 26(3): 1248–1258. https://doi.org/10.1111/gcb.14930

Gower JC (1971) 27 A general coefficient of similarity and some of its properties. Biometrics 27(4): 857–871. https://doi.org/10.2307/2528823

Grenié M, Denelle P, Tucker CM, Munoz F, Violle C (2017) funrar: An R package to characterize functional rarity. Diversity & Distributions 23(12): 1365–1371. https://doi.org/10.1111/ddi.12629

HELCOM (2018) Status of coastal fish communities in the Baltic Sea during 2011–2016 - the third thematic assessment.

HELCOM (2019) Guidelines for coastal fish monitoring. https://helcom.fi/wp-content/uploads/2020/01/HELCOM-Guidelines-for-coastal-fish-monitoring-2019.pdf [June 21, 2023]

HELCOM (2023) Thematic assessment of hazardous substances, marine litter, underwater noise and non-indigenous species 2016–2021. Helsinki Commission (HELCOM). 190.

Hess S, Fischer S, Taborsky B (2016) Territorial aggression reduces vigilance but increases aggression towards predators in a cooperatively breeding fish. Animal Behaviour 113: 229–235. https://doi.org/10.1016/j.anbehav.2016.01.008

Hillebrand H, Bennett DM, Cadotte MW (2008) Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. Ecology 89(6): 1510–1520. https://doi.org/10.1890/07-1053.1

Hirsch PE, N'Guyen A, Adrian-Kalchhauser I, Burkhardt-Holm P (2016) What do we really know about the impacts of one of the 100 worst invaders in Europe? A reality check. Ambio 45(3): 267–279. https://doi.org/10.1007/s13280-015-0718-9

Huntingford FA (1976) The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, Gasterosteus Aculeatus. Animal Behaviour 24(2): 245–260. https://doi.org/10.1016/S0003-3472(76)80034-6

ICES (2022a) Baltic Sea Ecoregion – Ecosystem overview. ICES Advice: Ecosystem Overviews, 24 pp. https://doi.org/10.17895/ICES.ADVICE.21725438

ICES (2022b) Workshop on stickleback and round goby in the Baltic Sea (WKSTARGATE). ICES Scientific Reports. [report] https://doi.org/10.17895/ices.pub.21345291.v2

IPBES (2023) Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES secretariat. https://doi.org/10.5281/zenodo.3553579

Jones JC, Reynolds JD (1999) Costs of egg ventilation for male common gobies breeding in conditions of low dissolved oxygen. Animal Behaviour 57(1): 181–188. https://doi.org/10.1006/anbe.1998.0939

Jude DJ (1997) Round gobies: Cyberfish of the third millennium. Great Lakes Research Review 3: 27–34.

Karlson AML, Almqvist G, Skóra KE, Appelberg M (2007) Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. ICES Journal of Marine Science 64(3): 479–486. https://doi.org/10.1093/icesjms/fsl049

Katsanevakis S, Wallentinus I, Zenetos A, Leppäkoski E, Çinar ME, Oztürk B, Grabowski M, Golani D, Cardoso AC (2014) Impacts of invasive alien marine species on ecosystem services and biodiversity: A pan-European review. Aquatic Invasions 9(4): 391–423. https://doi.org/10.3391/ai.2014.9.4.01

Kornis MS, Mercado-Silva N, Vander Zanden MJ (2012) Twenty years of invasion: A review of round goby *Neogobius melanostomus* biology, spread and ecological implications. Journal of Fish Biology 80(2): 235–285. https://doi.org/10.1111/j.1095-8649.2011.03157.x

Kotta J, Nurkse K, Puntila R, Ojaveer H (2016) Shipping and natural environmental conditions determine the distribution of the invasive non-indigenous round goby *Neogobius melanostomus* in a regional sea. Estuarine, Coastal and Shelf Science 169: 15–24. https://doi.org/10.1016/j.ecss.2015.11.029

Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM (2015) Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29: 592–599. https://doi.org/10.1111/1365-2435.12345

Kruze E, Avotins A, Rozenfelde L, Putnis I, Sics I, Briekmane L, Olsson J (2023) The population development of the invasive round goby *Neogobius melanostomus* in latvian waters of the Baltic Sea. Fishes 8(6): 305. https://doi.org/10.3390/fishes8060305

Leppäkoski E, Gollasch S, Gruszka P, Ojaveer H, Olenin S, Panov V (2002) The Baltic - A sea of invaders. Canadian Journal of Fisheries and Aquatic Sciences 59(7): 1175–1188. https://doi.org/10.1139/f02-089

Liaw A, Wiener M (2002) Classification and Regression by randomForest. R News: 2.

Lindegren M, Thomas MK, Jónasdóttir SH, Nielsen TG, Munk P (2020) Environmental niche separation promotes coexistence among ecologically similar zooplankton species—North Sea copepods as a case study. Limnology and Oceanography 65(3): 545–556. https://doi.org/10.1002/lno.11322

Lindegren M, Gabellini AP, Munk P, Edelvang K, Hansen FT (2022) Identifying key processes and drivers affecting the presence of non-indigenous marine species in coastal waters. Biological Invasions 24(9): 2835–2850. https://doi.org/10.1007/s10530-022-02802-w

Litchman E, Klausmeier CA (2008) Trait-based community ecology of phytoplankton. Annual Review of Ecology, Evolution, and Systematics 39(1): 615–639. https://doi.org/10.1146/annurev.ecolsys.39.110707.173549

Litchman E, Ohman MD, Kiørboe T (2013) Trait-based approaches to zooplankton communities. Journal of Plankton Research 35(3): 473–484. https://doi.org/10.1093/plankt/fbt019

Lodge DM, Simonin PW, Burgiel SW, Keller RP, Bossenbroek JM, Jerde CL, Kramer AM, Rutherford ES, Barnes MA, Wittmann ME, Chadderton WL, Apriesnig JL, Beletsky D, Cooke RM, Drake JM, Egan SP, Finnoff DC, Gantz CA, Grey EK, Hoff MH, Howeth JG, Jensen RA, Larson ER, Mandrak NE, Mason DM, Martinez FA, Newcomb TJ, Rothlisberger JD, Tucker AJ, Warziniack TW, Zhang H (2016) Risk Analysis and Bioeconomics of Invasive Species to Inform Policy and Management. Annual Review of Environment and Resources 41(1): 453–488. https://doi.org/10.1146/annurev-environ-110615-085532

Matern S, Herrmann J-P, Temming A (2021) Differences in diet compositions and feeding strategies of invasive round goby *Neogobius melanostomus* and native black goby *Gobius niger* in the Western Baltic Sea. Aquatic Invasions 16(2): 314–328. https://doi.org/10.3391/ai.2021.16.2.07

Mathakutha R, Steyn C, Roux PC le, Blom IJ, Chown SL, Daru BH, Ripley BS, Louw A, Greve M (2019) Invasive species differ in key functional traits from native and non-invasive alien plant species. Journal of Vegetation Science 30: 994–1006. https://doi.org/10.1111/jvs.12772

Meunier B, Yavno S, Ahmed S, Corkum LD (2009) First documentation of spawning and nest guarding in the laboratory by the invasive fish, the round goby (*Neogobius melanostomus*). Journal of Great Lakes Research 35(4): 608–612. https://doi.org/10.1016/j.jglr.2009.08.012

Millennium Ecosystem Assessment (Program) [Ed.] (2005) Ecosystems and human well-being: wetlands and water synthesis: a report of the Millennium Ecosystem Assessment. World Resources Institute, Washington, DC, 68 pp.

Momigliano P, Denys GPJ, Jokinen H, Merilä J (2018) *Platichthys solemdali* sp. nov. (Actinopterygii, Pleuronectiformes): A New Flounder Species From the Baltic Sea. Frontiers in Marine Science 5: 225. https://doi.org/10.3389/fmars.2018.00225

Montanyès M, Weigel B, Lindegren M (2023) Community assembly processes and drivers shaping marine fish community structure in the North Sea. Ecography 2023(10): e06642. https://doi.org/10.1111/ecog.06642

Nõomaa K, Kotta J, Szava-Kovats R, Herkül K, Eschbaum R, Vetemaa M (2022) Novel fish predator causes sustained changes in its prey populations. Frontiers in Marine Science 9: 849878. https://doi.org/10.3389/fmars.2022.849878

Ojaveer H, Jaanus A, Mackenzie BR, Martin G, Olenin S, Radziejewska T, Telesh I, Zettler ML, Zaiko A (2010) Status of biodiversity in the Baltic sea. PLoS ONE 5(9): 1–19. https://doi.org/10.1371/journal.pone.0012467

Ojaveer H, Olenin S, Narščius A, Florin A-B, Ezhova E, Gollasch S, Jensen KR, Lehtiniemi M, Minchin D, Normant-Saremba M, Strāke S (2017) Dynamics of biological invasions and pathways over time: A case study of a temperate coastal sea. Biological Invasions 19(3): 799–813. https://doi.org/10.1007/s10530-016-1316-x

Olenin S, Gollasch S, Lehtiniemi M, Sapota M, Zaiko A (2017) Biological invasions. In: Snoeijs-Leijonmalm P, Schubert H, Radziejewska T (Eds) Biological Oceanography of the Baltic Sea. Springer Netherlands, Dordrecht, 193–232. https://doi.org/10.1007/978-94-007-0668-2_5

Olsson J (2019) Past and current trends of coastal predatory fish in the Baltic Sea with a focus on perch, pike, and pikeperch. Fishes 4(1): 7. https://doi.org/10.3390/fishes4010007

Olsson J, Bergström L, Gårdmark A (2012) Abiotic drivers of coastal fish community change during four decades in the Baltic Sea. ICES Journal of Marine Science 69(6): 961–970. https://doi.org/10.1093/icesjms/fss072

Paavola M, Olenin S, Leppäkoski E (2005) Are invasive species most successful in habitats of low native species richness across European brackish water seas? Estuarine, Coastal and Shelf Science 64(4): 738–750. https://doi.org/10.1016/j.ecss.2005.03.021

Pavoine S, Vallet J, Dufour AB, Gachet S, Daniel H (2009) On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. Oikos 118(3): 391–402. https://doi.org/10.1111/j.1600-0706.2008.16668.x

Pecuchet L, Törnroos A, Lindegren M (2016) Patterns and drivers of fish community assembly in a large marine ecosystem. Marine Ecology Progress Series 546: 239–248. https://doi.org/10.3354/meps11613

Pecuchet L, Lindegren M, Hidalgo M, Delgado M, Esteban A, Fock HO, Gil de Sola L, Punzón A, Sólmundsson J, Payne MR (2017) From traits to life-history strategies: Deconstructing fish community composition across European seas. Global Ecology and Biogeography 26(7): 812–822. https://doi.org/10.1111/geb.12587

Puntila-Dodd R, Florin A-B, Naddafi R, Behrens JW, Kotta J, Smolinski S, Wozniczka A (2018) Abundance and distribution of round goby (*Neogobius melanostomus*).

Puntila-Dodd R, Bekkevold D, Behrens JW (2021) Estimating salinity stress via hsp70 expression in the invasive round goby (*Neogobius melanostomus*): Implications for further range expansion. Hydrobiologia 848(2): 421–429. https://doi.org/10.1007/s10750-020-04449-x

Quell F, Schratzberger M, Beauchard O, Bruggeman J, Webb T (2021) Biological trait profiles discriminate between native and non-indigenous marine invertebrates. Aquatic Invasions 16(4): 571–600. https://doi.org/10.3391/ai.2021.16.4.01

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [URL] http://www. R-project.org

Reusch TBH, Dierking J, Andersson HC, Bonsdorff E, Carstensen J, Casini M, Czajkowski M, Hasler B, Hinsby K, Hyytiäinen K, Johannesson K, Jomaa S, Jormalainen V, Kuosa H, Kurland S, Laikre L, MacKenzie BR, Margonski P, Melzner F, Oesterwind D, Ojaveer H, Refsgaard JC, Sandström A, Schwarz G, Tonderski K, Winder M, Zandersen M (2018) The Baltic Sea as a time machine for the future coastal ocean. Science Advances 4(5): eaar8195. https://doi.org/10.1126/sciadv.aar8195

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs 83(3): 263–282. https://doi.org/10.1890/13-0183.1

Ricotta C, Godefroid S, Rocchini D (2010) Patterns of native and exotic species richness in the urban flora of Brussels: rejecting the 'rich get richer' model. Biological Invasions 12: 233–240. https://doi.org/10.1007/s10530-009-9445-0

Rilov G, Crooks JA (2009) 204 Biological Invasions in Marine Ecosystems. https://doi.org/10.1007/978-3-540-79236-9

Schwartzbach A, Behrens JW, Svendsen JC, Nielsen P, van Deurs M (2020) Size-dependent predation of round goby *Neogobius melanostomus* on blue mussels *Mytilus edulis*. Fisheries Management and Ecology 27(3): 215–218. https://doi.org/10.1111/fme.12400

Skabeikis A, Morkūnė R, Bacevičius E, Lesutienė J, Morkūnas J, Poškienė A, Šiaulys A (2019) Effect of round goby (*Neogobius melanostomus*) invasion on blue mussel (*Mytilus edulis trossulus*) population and winter diet of the long-tailed duck (*Clangula hyemalis*). Biological Invasions 21(3): 911–923. https://doi.org/10.1007/s10530-018-1869-y

Skóra KE, Stolarski J (1993) *Neogobius melanostomus* (Pallas 1811) a new immigrant species in Baltic Sea. Proceedings of the Second International Estuary Symposium held in Gdańsk, 18–22.

Steger J, Bošnjak M, Belmaker J, Galil BS, Zuschin M, Albano PG (2022) Non-indigenous molluscs in the Eastern Mediterranean have distinct traits and cannot replace historic ecosystem functioning. Global Ecology and Biogeography 31(1): 89–102. https://doi.org/10.1111/geb.13415

Törnroos A, Bonsdorff E (2012) Developing the multitrait concept for functional diversity: Lessons from a system rich in functions but poor in species. Ecological Applications 22(8): 2221–2236. https://doi.org/10.1890/11-2042.1

Törnroos A, Bonsdorff E, Bremner J, Blomqvist M, Josefson AB, Garcia C, Warzocha J (2015) Marine benthic ecological functioning over decreasing taxonomic richness. Journal of Sea Research 98: 49–56. https://doi.org/10.1016/j.seares.2014.04.010

Törnroos A, Pecuchet L, Olsson J, Gårdmark A, Blomqvist M, Lindegren M, Bonsdorff E (2019) Four decades of functional community change reveals gradual trends and low interlinkage across trophic groups in a large marine ecosystem. Global Change Biology 25(4): 1235–1246. https://doi.org/10.1111/gcb.14552

van Deurs M, Moran NP, Schreiber Plet-Hansen K, Dinesen GE, Azour F, Carl H, Møller PR, Behrens JW (2021) Impacts of the invasive round goby (*Neogobius melanostomus*) on benthic invertebrate fauna: A case study from the Baltic Sea. NeoBiota 68: 19–30. https://doi.org/10.3897/neobiota.68.67340

Viana IG, Siriwardane-de Zoysa R, Willette DA, Gillis LG (2019) Exploring how non-native seagrass species could provide essential ecosystems services: A perspective on the highly invasive seagrass *Halophila stipulacea* in the Caribbean Sea. Biological Invasions 21: 1461–1472. https://doi.org/10.1007/s10530-019-01924-y

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116(5): 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Violle C, Thuiller W, Mouquet N, Munoz F, Kraft NJB, Cadotte MW, Livingstone SW, Mouillot D (2017) Functional rarity: The ecology of outliers. Trends in Ecology & Evolution 32(5): 356–367. https://doi.org/10.1016/j.tree.2017.02.002

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as Global Environmental Change.

Vivó-Pons A, Alós J, Tomas F (2020) Invasion by an ecosystem engineer shifts the abundance and distribution of fish but does not decrease diversity. Marine Pollution Bulletin 160: 111586. https://doi.org/10.1016/j.marpolbul.2020.111586

Vivó-Pons A, Blomqvist M, Törnroos A, Lindegren M (2023) A trait-based approach to assess niche overlap and functional distinctiveness between non-indigenous and native species. Ecology Letters 26(11): 1911–1925. https://doi.org/10.1111/ele.14315

Voipio A (1981) 30 The Baltic Sea. Elsevier B.V., Helsinki, 418 pp.

Wallin-Kihlberg I, Florin A-B, Lundström K, Östman Ö (2023) Detection of multiple fish species in the diet of the invasive round goby reveals new trophic interactions in the Baltic Sea. Aquatic Invasions 18(2): 141–162. https://doi.org/10.3391/ai.2023.18.2.104960

Wickett RG, Corkum LD (1998) Nest defense by the non-indigenous fish, the round goby, *Neogobius melanostomus* (Gobiidae), on a shipwreck in western Lake Erie. Canadian Field Naturalist 112: 653–656.

Wood SN (2017) Generalized Additive Models: An Introduction with R, Second Edition Generalized additive models: An introduction with R, 2nd edn. CRC Press, 476 pp. https://doi.org/10.1201/9781315370279

Xu M, Li S, Dick JTA, Gu D, Fang M, Yang Y, Hu Y, Mu X (2022) Exotic fishes that are phylogenetically close but functionally distant to native fishes are more likely to establish. Global Change Biology 28(19): 5683–5694. https://doi.org/10.1111/gcb.16360

Zobel M (1997) The relative role of species pools in determining plant species richness: An alternative explanation of species coexistence? Trends in Ecology & Evolution 12(7): 266–269. https://doi.org/10.1016/S0169-5347(97)01096-3

Supplementary material 1

Supplementary information

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Data type: docx

Explanation note: **table S1.** List of the different modalities for the diet trait. The colored cells indicate the specific modality combination that is displayed by a certain number of species within the regional pool. Numbers inside colored cells indicate the probability that a certain species displays such modality. **table S2.** Trait values for all fish species. The included traits and modalities are further described in Table 1. **table S3.** Functional distinctiveness, WPUE and relative WPUE of the fish species present in the regional pool starting from the most distinct taxon. Quartiles used to classify species distinctiveness are also included. Round goby is highlighted in bold. **table S4.** Importance of predictors for the fitted GAMM and RF. **figure S1.** Correlation between model-derived and in-situ data of bottom temperatureand bottom salinity. **figure S2.** Plots showing the comparison between variance explained and mean squared error (MSE) between GAMM and RF after the cross-validation process.

Link: https://doi.org/10.3897/neobiota.89.110203.suppl1